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Sequence and analysis of the DNA encoding protective antigen of *Bacillus anthracis*.

Welkos SL, Lowe JR, Eden-McCutchan F, Vodkin M, Leppla SH, Schmidt JJ.

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Bacteriology Division, U.S. Army Medical Research Institute of Infectious Diseases, Frederick, MD 21701-5011.

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The nucleotide sequence of the protective antigen (PA) gene from *Bacillus anthracis* and the 5' and 3' flanking sequences were determined. PA is one of three proteins comprising anthrax toxin; and its nucleotide sequence is the first to be reported from *B. anthracis*. The open reading frame (ORF) is 2319 bp long, of which 2205 bp encode the 735 amino acids of the secreted protein. This region is preceded by 29 codons, which appear to encode a signal peptide having characteristics in common with those of other secreted proteins. A consensus TATAAT sequence was located at the putative -10 promoter site. A Shine-Dalgarno site similar to that found in genes of other *Bacillus* sp. was located 7 bp upstream from the ATG start codon. The codon usage for the PA gene reflected its high A + T (69%) base composition and differed from those of genes for bacterial proteins from most other sequences examined. The TAA translation stop codon was followed by an inverted repeat forming a potential termination signal. In addition, a 192-codon ORF of unknown significance, theoretically encoding a 21.6-kDa protein, preceded the 5' end of the PA gene.

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J. Bacteriol., 02 1994, 586-595, Vol 176, No. 3
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Regulation of the *Bacillus anthracis* protective antigen gene: CO₂ and a trans-acting element activate transcription from one of two promoters

T M Koehler, Z Dai and M Kaufman-Yarbray

Department of Microbiology and Molecular Genetics, Medical School, University of Texas, Houston 77030.

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The pag gene of *Bacillus anthracis*, located on plasmid pXO1 (185 kb), encodes protective antigen, a component of the anthrax lethal and edema toxins. Synthesis of protective antigen is enhanced during growth of the organism with elevated levels of CO₂. The CO₂ effect is at the level of transcription, and pXO1-encoded regulatory factors have been implicated in control of pag expression. We used a Tn917-LTV3 insertion mutant of *B. anthracis* in which the wild-type pag gene on pXO1 was replaced with a pag-lacZ transcriptional fusion to monitor pag promoter activity. Expression of the pag-lacZ fusion is induced five- to eightfold during growth in 5% CO₂ compared with growth in air. Growth in 20% CO₂ increases transcription up to 19-fold. By monitoring pag-lacZ expression in atmospheres with different O₂ and CO₂ concentrations, we demonstrated definitively that the CO₂ effect is specific and not simply a result of increased anaerobiosis. The results of 5' end mapping of pag transcripts indicate multiple sites of transcript initiation. We have determined two major apparent start sites, designated P1 and P2, located at positions -58 and -26 relative to the translation initiation codon, respectively. Analysis of total RNA from late-log-phase cells shows comparable initiation from P1 and P2 in wild-type strains grown in aerobic conditions. However, initiation from P1 is increased approximately 10-fold in cultures grown with an elevated level (5%) of CO₂. We have identified a locus on pXO1, more than 13 kb upstream from the pag gene, which enhances pag transcription. When added in trans, this locus increases the level of transcripts with 5' ends mapping to P1 but has no effect on the level of transcripts with 5' ends mapping to P2. The CO₂ effect on P1 is observed only in the presence of the activator locus.

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